biological sciences, Professor Minot, of Harvard University. The Association is promised a welcome by the Governor of the State, the Mayor of Denver and other dignitaries, and the people of the city are noted for their hospitality.

A few words in regard to routes may be of service to members in the East. The way to Denver is either by Chicago or St. Louis, the former being the quicker. Chicago may be reached from New York in about twenty-four hours by the Pennsylvania and New York Central Railways. For example, a train leaving New York at 7:55 A. M. by the Pennsylvania reaches Chicago at 7:45 the next morning, or a train leaving New York at 5:30 P. M. by the New York Central and Lake Shore reaches Chicago at 4:30 the next afternoon. The best train from Chicago leaves at 10 A. M. by the Chicago and Northwestern; at 1 P. M. by the Rock Island Route and 4 P. M. by the Burlington, reaching Denver at 1:40, 4:45 and 6:30, respectively, the next afternoon. Those who leave Chicago on Saturday, the twenty-fourth, by one of these trains will doubtless travel in good company. The rate from New York to Denver and return at one and one-third fare would be about $65; the ordinary fare to Chicago and return is $40, and the return ticket from Chicago to Denver is $31.50. The latter method is not much dearer than the former and may be cheaper to members living west of New York. It is more convenient, as the tickets from Chicago may be purchased as early as August 10 and are good for return until October 31, and the route to Chicago may be varied and a stop may be made at Buffalo or elsewhere. The headquarters of the Association are at the Brown Palace Hotel, and those wanting rooms should engage them in advance. There are, however, a number of good hotels at Denver.

Everyone knows that Denver is one of the great centers for excursions of scientific and general interest. The geologists, under the leadership of Professor Van Hise, have planned a ten days' excursion before the meeting. Other excursions of interest to chemists, engineers, geologists, zoologists, botanists, anthropologists and indeed to all members of the Association may be made during the meeting or at its close. It is sufficient to mention Pike's Peak, the Garden of the Gods, and the Grand Canyon of the Colorado, to all of which excursions have been planned. The trip to Colorado should be made by everyone and should be made now by all members of the American Association for the Advancement of Science.

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*REGENERATION AND LIABILITY TO INJURY.**

THERE is a widespread belief amongst zoologists that a definite relation exists between the liability of an animal to injury and its power of regeneration. It is also supposed that those individual parts of an animal that are more exposed to accidental injury, or to the attacks of enemies, are the parts in which regeneration is best developed, and conversely, that those parts of the body that are rarely or never injured do not possess the power of regeneration.

Not only do we find this belief implied in many ways, but we find this point of view definitely taken by several eminent

* One of a course of lectures on 'Regeneration' delivered at Columbia University, and shortly to be published in the Columbia University *Biological Series*.

writers, and in some cases carried so far that the process of regeneration itself is supposed to be accounted for by the liability of the parts to injury. In order that it may not appear that I have exaggerated the widespread occurrence of this belief a few examples may be cited.

Réaumur in 1742 pointed out that regeneration is especially characteristic of those animals whose body is liable to be broken, or, as in the earthworm, subject to the attacks of enemies. Bonnet (1745) thought that such a connection exists as has been already stated, and that the animals that possess the power of regeneration have been endowed with germs set aside for this very purpose. He further believed that there would be in each animal that regenerates as many of these germs as the number of times that it is liable to be injured during its natural life. Darwin in his book on 'Animals and Plants under Domestication' says: "In the case of those animals that may be bisected, or chopped into pieces, and of which every fragment will reproduce the whole, the power of re-growth must be diffused throughout the whole body. Nevertheless, there seems to be much truth in the view maintained by Professor Lessona * that this capacity is generally a localized and special one serving to replace parts which are eminently liable to be lost in each particular animal. The most striking case in favor of this view is that the terrestrial salamander, according to Lessona, can not reproduce lost parts, whilst another species of the same genus, the aquatic salamander, has extraordinary powers of re-growth, as we have just seen; and this animal is eminently liable to have its limbs, tail, eyes and jaws bitten off by other tritons."

Lang, referring to the brittleness of the tails of lizards, points out that this is a very useful character, since the bird of prey that has struck at a lizard gets hold of only the last part of the animal to disappear under cover; the lizard escapes by breaking off its tail. The brittleness of the tail is, therefore, an adaptive character that has become fixed by long inheritance.

To this example may be added that of certain land snails of the Philippine Islands. The individuals of the genus helicarion live on trees in damp forests, often in great droves. They are very active, and creep with unusual swiftness over the stems and leaves of the trees. Semper has recorded that all the species observed by him have the remarkable power of breaking off the tail (foot) close behind the shell, if the tail is roughly grasped. A convulsive movement is made until the tail comes off, and the snail drops to the ground, where it is concealed by the leaves. Semper adds that in this way the snails often escaped from him, and from his collectors, leaving nothing behind but their tails. The tail is said to be the most obvious part of the animal, and it is assumed that this is, therefore, the part that a reptile or bird would first attack.* Lang states that in this case external influences have produced an extraordinarily well developed sensitiveness in the animal, so that it reacts to the external stimulus by voluntarily throwing off the tail. It would be, of course, of small advantage to be able to throw off the tail un-

* Delage and Giard give Lessona (1869) the credit for first stating that the phenomenon of regeneration is an adaptation to liability to injury; but Réaumur first suggested this idea in 1742 and Bonnet in 1745. Delage's interpretation, viz., that Lessona ascribed this to a '*prévoyance de la nature*' has been denied by Lessona's biographer, Camerano ('La Vita di M. Lessona' *Acad. R. d. Torino* (2), XLV., 1896) and by Giard ('Sur L'autotomie Parasitaire,' etc., *Compt. Rendus de Séances de la Societé de Biologie*, May, 1897).

* Whether, having once failed in this way to obtain the snail, the bird or lizard would not learn to make a frontal attack is not stated. Or shall we assume the tail is all that is wanted?

less the power of regenerating the lost organ existed, or was acquired at the same time as the extreme sensitiveness that brings about the reaction. Lang does not state, however, explicitly that he believes the regenerative power to have arisen through the exposure of the tail of the lizard and the tail of the snail to injury, although he thinks that the mechanism by means of which these parts are thrown off has been acquired in this way. Several other writers have, however, used these same cases to illustrate the supposed principle of liability to injury and power of regeneration.

Weismann in his book on 'The Germ Plasm' has adopted the principle of a connection between regeneration and liability to injury and has carried it much further than have other writers. We can, therefore, most profitably make a careful examination of Weismann's position. His general idea may be gathered from the following quotation:* "The dissimilarity, moreover, as regards the power of regeneration *in various members of the same species*, also indicates that adaptation is an important factor in the process. In proteus which in other respects possesses so slight a capacity for regeneration, the gills grow again rapidly when they have been cut off. In lizards again this power is confined to the tail, and the limbs cannot become restored. In these animals, however, the tail is obviously far more likely to become mutilated than are the limbs, which, as a matter of fact, are seldom lost, although individuals with stumps of legs are occasionally met with. The physiological importance of the tail of a lizard consists in the fact that it preserves the animal from total destruction, for pursuers will generally aim at the long trailing tail,† and thus the animal often escapes, as the tail breaks off when it is firmly seized. It is, in fact, as Leydig was the first to point out, specially adapted for breaking off, the bodies of the caudal vertebræ from the seventh onward being provided with a special plane of fracture so that they easily break into two transversely. Now if this capability of fracture is provided for by a special arrangement and modification of the parts of the tail, we shall not be making too daring an inference if we regard the regenerative power of the tail as *a special adaptation, produced by selection, of this particular part of the body, the frequent loss of which is in a certain measure provided for*, and not as the outcome of an unknown 'regenerative power' possessed by the entire animal. This arrangement would not have been provided if the part had been of no, or only of slight, physiological importance, as is the case in snakes and chelonians, although these animals are as highly organized as lizards. The reason that the limbs of lizards are not replaced is, I believe, due to the fact that these animals are seldom seized by the leg, owing to their extremely rapid movements." Overlooking the numerous cases of the regeneration of internal organs that have been known for several years, and basing his conclusion on a small, unconvincing experiment of his own on the lungs of a few salamanders, Weismann concludes: "Hence there is no such thing as a general power of regeneration; in each kind of animal this power is graduated according to the need of regeneration in the part under consideration; that is to say, the degree in which it is present is mainly in proportion to the liability of the part to injury."

After arriving at this conclusion the following admission is a decided anticlimax: "The question, however, arises as to whether the capacity of each part for regeneration results from special process of adaptation, or whether regeneration occurs

* 'The Germ-Plasm.' Translation by W. Newton Parker, 1893, page 116.

† There are no facts that show that this statement is not entirely imaginary. T. H. M.

as the mere outcome—which is to some extent unforeseen—of the physical nature of an animal. Some statements which have been made on this subject seem hardly to admit of any but the latter explanation." After showing that some newts confined in aquaria attacked each other, "and several times one of them seized another by the lower jaw, and tugged and bit at it so violently that *it would have been torn off if I had not separated the animals*,"* and after referring to the regeneration of the stork's beak, Weismann concludes: "Such cases, the accuracy of which can scarcely be doubted, indicate that the capacity for regeneration does not depend only on the special adaptation of a particular organ, but that a general power also exists which belongs to the whole organism, and to a certain extent affects many and perhaps even all parts. By virtue of this power, moreover, simple organs can be replaced when they are not specially adapted for regeneration." The perplexity of the reader, as a result of this temporary vacillation on Weismann's part, is hardly set straight by the general conclusion that follows on the same page: "We are, therefore, led to infer that the general capacity of all parts for regeneration may have been acquired by selection in the lower and simpler forms, and that it gradually decreased in the course of phylogeny in correspondence with the increase in complexity of organization; but that it may, on the other hand, be increased by special selective processes in each stage of its degeneration, in the case of certain parts which are physiologically important and are at the same time frequently exposed to loss."

There are certain statements of facts in this chapter that are incorrect, and the argument is so loose and vague that it is difficult to tell just what is really meant. As a misstatement of fact I may select the following case. It is stated that lumbriculus does not have the power of regenerating laterally if cut in two, and it is argued that a small animal of this form could rarely be injured at the side without cutting the animal completely in two. As a matter of fact, lumbriculus can regenerate laterally, and very perfectly, as any one can verify if he takes the trouble to perform the experiment; but, of course, if the whole animal is split in two lengthwise the pieces die, or if a very long piece is split from one side the remaining piece usually disintegrates. If, however, the anterior end is split in two for a short distance, or if a piece is partially split in two, the half remaining in contact with the rest of the piece completes itself laterally. The same result follows also in the earthworm.

As an example of looseness of expression I may quote the following from Weismann: "A useless or almost useless rudimentary part may often be injured or torn off *without causing processes of selection to occur which would produce in it a capacity for regeneration.* The tail of a lizard again, which is very liable to injury, becomes regenerated because as we have seen it is of great importance to the individual and if lost its owner is placed at a disadvantage." And as an example of vagueness, the following statement commends itself: "Finally the complexity of the individual parts constitutes the third factor which is concerned in regulating the regenerative power of the part in question; for the more complex the structure is, the longer and the more energetically the process of selection must act in order to provide the mechanism of regeneration, which consists in the equipment of a large number of different kinds of cells with the supplementary determinants which are accurately graduated and regulated as regards their power of multiplication."

Without attempting to disentangle the ideas that are involved in these sentences,

* The *italics* are, of course, my own. T. H. M.

let us rather attempt to get at a general idea of Weismann's views. In a later paper (1900), in reply to certain criticisms, he has stated his position somewhat more lucidly. In the following statement I have tried to give the essential part of his hypotheses: Weismann believes the process of regeneration to be regulated by 'natural selection'; in fact, he states that it has arisen through such a process in the lower animals—since they are more subject to injury—and that it has been lost in the higher forms except where, on account of injury, it has been retained in certain parts. Thus when Weismann speaks of regeneration as being an adaptation of the organism to its environment, we must understand him to mean that this adaptation is the result of the action of natural selection. We should be on our guard not to be misled by the statement that because regeneration is useful to the animal, it has been acquired by natural selection, since it is possible that regeneration might be more or less useful without in any way involving the idea that natural selection is the originator of this or of any other adaptation. It will be seen, therefore, that in order to meet Weismann on his own ground it will be necessary to have a clear understanding in regard to the relation of regeneration to Darwin's principle of natural selection. With Weismann's special hypothesis of the 'mechanism,' so-called, by which regeneration is made possible we have here nothing to do, but may consider it on its own merits in another chapter.

In order to have before us the material for a discussion of the possible influence of natural selection on regeneration, let us first examine the facts that bear on the question of the liability of the parts to injury and their power to regenerate, and in this connection the questions concerning the renewal of parts that are thrown off by the animals themselves in response to an external stimulus are worthy of careful consideration. A comparison between the regeneration of these parts with that of other parts of the same animal gives also important data. Furthermore, a comparison may be made between different parts of the same animal, or between the same parts of different animals living under similar or under dissimilar conditions.

There are only a few cases known in which a systematic examination has been carried out of the power of regeneration of the different parts of the body of the same animal. Spallanzani's results show that those salamanders that can regenerate their forelegs can regenerate their hind legs also. Towle, who has examined in my laboratory the regeneration of a number of American newts and salamanders, finds also that both the fore and hind legs regenerate in the same forms. The tail and the gills, in those newts with external gills, also regenerate. It has also been shown in triton that the eye regenerates if a portion of the bulb is left. Broussonet first showed (1786) that the fins of fish have the power to regenerate, although, strangely enough, Fraisse and Weismann state that very little power of regeneration is present in the fins of fish. I have found that the fins of several kinds of fish regenerate, belonging to widely different families.* In *Fundulus heteroclitus* I have found that the pectoral, pelvic, caudal, anal, and dorsal fins have the power of regeneration. In reptiles the feet do not regenerate, at least no cases are known, but the tail of lizards has this power well developed. In birds neither the wings nor the feet regenerate, but Fraisse has recorded the case of a stork in which, the lower jaw being broken off, and the upper being cut off at the same level, both regenerated. Bordage has recorded the re-

* Fundulus heteroclitus, Stenopus chrysops, Decapterus macrella, Menticirrhus macrella, Carassius auratus, Phoxinus funduloides, Noturus sp., and a few others.

generation of the beak of the domesticated fighting cocks (of the Malay breed) of Mauritius. In the mammals neither the legs nor the tail, nor the jaws regenerate, although several of the internal organs, as described in the next chapter, have extensive powers of regeneration.

The best opportunity to examine the regenerative power in similar organs of the same animal is found in forms like the crustacea, myriapods and insects in which external appendages are repeated in each or many segments of the body. In decapod crustacea, including shrimps, lobsters, crayfish, crabs, hermit-crabs, etc., regeneration takes place in the walking legs of all the forms that have been examined, and this includes members of many genera and families. I have made a special examination of the regeneration of the appendages of the hermit-crab. In this animal, which lives in an appropriated snail's shell, only the anterior part of the body projects from the shell. The part that protrudes is covered by a hard cuticle, while the part of the body covered by the shell is quite soft. Three pairs of legs are protruded from the shell. The first pair with large claws are used for procuring food, and as organs of offense and defense; the second and third pairs are used for walking. The following two pairs that correspond to the last two pairs of walking legs of crabs and crayfishes, are small, and are used by the animal in bracing itself against the shell. The first three pairs of legs have an arrangement at the base, the 'breaking-joint,' by means of which the leg is thrown off, if injured. The last two pairs of thoracic legs can not be thrown off. The first three pairs of legs are often lost under natural conditions. In an examination of 188 individuals I found that 21 (or 11 per cent.) had lost one or more legs. If one of the first three legs is injured, except in the outer segment, it is thrown off at the breaking-joint, and a new leg regenerates from the broken-off end of the stump that is left. The new leg does not become full size, and is of little use until the crab has moulted at least once. The leg breaks off so close to the body, and the part inside of the breaking-joint is so well protected by the bases of the other legs, that it is scarcely possible that the leg could be torn off inside of the breaking-joint, and, as a matter of observation, all crabs that are found regenerating these legs under natural conditions do so from the breaking-joint. If, however, by means of small scissors, the leg is cut off quite near the body, a new leg regenerates from the cut end, even when the leg is cut off at its very base. The breaking-joint would thoroughly protect from injury the part of the leg that lies nearer to the body, and yet from this inner part a new leg is regenerated. Moreover, the new leg is perfect in every respect, even to the formation of a new breaking-joint. In this case we have a demonstration that there need be no connection between the liability of a part to injury and its power of regeneration.

In still another way the same thing may be shown. If the crab is anesthetized, and a leg cut off outside of the breaking-joint it is not, at the time, thrown off—the nervous system, through whose action the breaking off takes place, being temporarily thrown out of order. After recovery, although the leg is thrown off in a large number of cases, it is sometimes retained. In such cases it is found that from the cut end the missing part is regenerated. In this case also we find that regeneration takes place from a part of the leg that can never regenerate under natural circumstances.

The third and fourth legs of the hermit-crab can not be thrown off, but they have the power of regeneration at any level at which they may be cut off. They are in a

position where they can seldom be injured, and I have never found them absent or injured in crabs caught in their natural environment. The soft abdomen is protected by the snail's shell. At the end of the abdomen the last pair of abdominal appendages serve as anchors to hold the crab in the shell. These appendages are large and very hard, and can seldom be injured unless the abdomen itself is broken, and under these circumstances the crab dies. Yet if these appendages are cut off they regenerate perfectly, and after a single moult can not be distinguished from normal ones.

The more anterior abdominal appendages are present only on one side of the adult, although they are present on both sides of the larva, and to judge from a comparison with other crustacea these appendages have degenerated completely on one side, and have become rudimentary in the male, even on the side on which they are present. These appendages regenerate if they are cut off. In the female the appendages are used to carry the eggs, and are, therefore, of use. They also have a similar power of regeneration. The maxillæ and maxillipeds of the hermit-crab have also the power of regeneration, as have also the two pairs of antennæ, and the eyes.

In other decapod crustacea also it has been shown that the power of regeneration of the appendages is well developed. It has been long known that the crayfish and the lobster can regenerate lost parts. The first pair of legs, or chelæ, in these forms has a breaking-joint, at which the leg can be thrown off, yet in the crayfish I have seen that if the leg is cut off inside of the breaking-joint it will regenerate. The four pairs of walking legs do not possess a breaking-joint, but may be thrown off in some cases at a corresponding level. They regenerate from this level, as well as nearer the body and further beyond this region. Pizibram has recently shown that, in a number of crustacea, regeneration of the appendages takes place, even when the entire leg is extirpated as completely as possible.

Newport has shown that the myriapods can regenerate their legs, and it is known that several forms have the power of breaking off their legs in a definite region at the base if the legs are injured, and I have observed in *Cermatia forceps* that this takes place even when the animal is thrown into a killing fluid. Newport (1844) has also shown that when the legs of a caterpillar are cut off new ones regenerate during the pupa stage. It has been long known* that the legs of mantis can regenerate, and Bordage, who has recently examined the question more fully, has shown that a breaking-joint is present at the base of the leg. The tarsus of the cockroach also regenerates, producing only four, instead of the five, characteristic segments.†

A number of writers have recorded the regeneration of the legs of spiders.‡ Schultz, who has recently examined more thoroughly the regeneration of the legs in some spiders, finds that the leg is renewed if cut off at any level. He removed the leg most often at the metatarsus, but also at the tibia, and generally between two joints. In some cases the leg was cut off at the coxa, at which level it is generally found to be lost under natural conditions. Wagner observed in tarantula that when the leg is removed at any other place than at the coxa the animal brings the wounded leg to its jaws, and bites it off down to the coxa. In the *Epeiridæ*, that Schultz chiefly made use of, this never happened. He observed,

* See Newport and Scudder.

† Brindley, '97.

‡ Lepelletur, *Nouveau Bulletin de la Société philomatique*, 1813, Tome III., page 254.

Heincken, *Zool. Journal*, 1829, Tome IV., page 284. (Also for insects, *ibid.*, page 294.)

Müller, *Manual de Physiol.*, Tome I., page 30.

Wagner, W., *Bull. Soc. Imp., Naturel.*, Moscow, '87.

however, even in these forms that when the leg is cut off at the coxa it regenerates better than when cut off at any other level. Schultz adds that we see here an excellent example of how regeneration is influenced by natural selection, since regeneration takes place best where the leg is most often broken off. On the other hand, the author hastens to add that since regeneration also takes place when the leg is cut off at any other level this shows that the power to regenerate is characteristic of all parts of the organism, and is not *only* a phenomenon of adaptation, as Weismann believes. It seems highly improbable that a spider could ever lose a leg in the middle of a segment, *i. e.*, between two joints, since the segments are hard and strong, and the joints much weaker, but nevertheless the leg has the power to regenerate also from the middle of the segment, if cut off in this region.

The formation of the new part takes place somewhat differently, according to Schultz, when the leg is amputated between two segments than when cut off at the coxa. In the latter case, there is produced from the cut end of the last segment a solid rod which, as it grows longer, bends on itself several times. Joints appear in the rod, beginning at the base. The leg is set free at the next moult. If the leg is cut off nearer the distal end a smaller rod is formed, that extends straight forward, or may be thrown into a series of folds. It lies, however, inside of the last segment, since the surface exposed by the cut is quickly covered over by a chitinous covering. The piece is set free at the next moult.

Loeb has found that if the body of the pycnogonid, *Phoxichilidium maxillare*, is cut in two there regenerates from the posterior end of the anterior half a new body-like outgrowth.

Without attempting to describe the many cases in worms and molluscs in which there is no obvious connection between the power of the part to regenerate and its liability to injury, but where it is more difficult to show that it may not exist, let us pass to an examination of the regeneration of the starfish. It has been known since the time of Réaumur that starfish have the power of regenerating new arms if the old ones are lost. It has been claimed that in certain starfishes an arm itself can produce a new starfish (Haeckel ('78), P. and R. Sarasin ('88), von Martens ('84) and Sars ('75)), but this has been denied by other observers. It has not been found to take place in several species of starfishes, but if a portion—even a small piece—of the disc is left with the arm a new disc and arms may develop (Fig. 38, F). When the arm of *Asterias vulgaris* is injured it pinches off in many cases at its base, and a new arm grows out from the short stump that remains. These same starfishes that are regenerating new arms in their natural environment have the new arms almost always arising from this breaking region.* Thus King found out of 1914 individuals of *Asterias vulgaris* collected at random, 206, or 10.7 per cent., had one or more new arms, and all these except one arose from near the disc. In other species it appears that the outer portions of the arm may be broken off without the rest of the arm being thrown off. King has found that in asterias, regeneration takes place

* The Sarasins have described several cases in *Linkia multiformis* in which an old arm has one or more new arms arising from it. In one case, copied in our Fig. 38, G, four rays arise from the end of one arm, producing the appearance of a new starfish. In fact the Sarasins interpret the result in this way, although they state that there is no madreporite on the upper surface, and they did not determine whether a mouth is formed at the convergence of the rays, because they did not wish to destroy so unique a specimen—even to find out the meaning of it. There seems to me little probability that the new structure is a starfish, but the old arm has been so injured that it has produced a number of new arms.

more rapidly from the base than at a more distal level. It may appear at first thought, that the more rapid regeneration of the arm at the place at which it is usually thrown off may be associated with its more frequent loss at this region—in other words, that the more rapid regeneration has been acquired by the region at which the arm is generally broken off. This interpretation is, however, excluded by the fact that, in general, the nearer to the base the arm is cut off, so much the more rapid is its regeneration. In other words, the more rapid regeneration of the arm at the base is only a part of a general law that holds throughout the arm. If the proposition is reversed, and it is claimed that the arm has acquired the property of breaking off at the base, because it regenerates more rapidly at that level, the following fact recorded by King is of importance, viz., that although the arm regenerates faster at the base, yet a new arm is not any sooner produced in this way, since there is more to be produced, and the new arm from the base may never catch up to one growing less rapidly from a more distal cut surface, but having a nearer goal to reach.

The results of our examination show that those forms that are liable to have certain parts of their bodies injured are able to regenerate not only these parts, but at the same time other parts of the body that are not subject to injury. The most remarkable instance of this sort is found in those animals having breaking-joints. We find in these forms that regeneration takes place both proximal and distal to this region. If the power of regeneration is connected with the liability of a part to injury, this fact is inexplicable.

If we turn now to the question as to whether regeneration takes place in those species that are subject to injury more frequently or better than in other species, we find that the data are not very complete or satisfactory for such an examination. It is not easy to tell to what extent different animals are exposed to injury. If we pass in review the main groups of the animal kingdom, we can at least gain some interesting facts in this connection.

In the Protozoa nucleated pieces have been found to regenerate in all forms that have been examined, including amœba, difflugia, thalassicolla, paramœcium, stentor, and a number of other ciliate infusoria.

In the sponges it has been found by Oscar Schmidt that pieces may produce new individuals, but how widely this occurs in the group is not known. In the cœlenterates many forms are known to regenerate, and it is not improbable that in one way or another the process occurs throughout the group. The hydroid forms, hydra, tubularia, parypha, eudendrium, antennularia, hydractinia, podocoryne, etc.; the jelly-fish, gonionemus, and certain members of the family *Thaumantidæ,* have been found to regenerate. Amongst the *Scyphozoa,* the metridium, cerianthus and the scyphistoma of aurelia regenerate and the jellyfishes belonging to this group have a limited amount of regenerative power.

In the Platodes we find all the triclads, that have been examined, including planaria, phagocata, dendrocælum, and the land triclad bipalium, regenerate. It has been shown that the marine triclads also regenerate, but less rapidly and extensively, while the marine polyclads have very limited power of regeneration. The regeneration of the trematodes and cestodes has not, so far as I know, been studied, neither have the nematodes been examined from this point of view.

Some of the nemerteans regenerate, others do not seem to have this power. A small fresh water form, tetrastemma, that I examined did not regenerate although some of the pieces, that were filled with eggs, remained alive for several months.

In the annelids we find a great many forms that regenerate—many marine polychæta have this power; all earthworms that have been studied regenerate; both land forms, as lumbricus, allolobophora, etc., and fresh-water forms, as lumbriculus, nais, tubifex, etc.

In the crustacea the appendages have the power to regenerate in all the forms that have been examined.

Several kinds of myriopods as well as a number of spiders are known to regenerate their legs. In the insects, however, only a few forms are known to have this power, as caterpillars, mantis and the cockroach. The large majority of insects, in the imago state, do not seem to be able to regenerate, although they have not been sufficiently examined.

In the molluscs regeneration of the head takes place under certain conditions. Spallanzani thought that if the entire head is cut off a new one regenerates. This conclusion was denied by at least eleven of his contemporaries and confirmed by about ten others. It was found later that the result depends in part on the time of year, and in part on the kind of snail. Carriere, who more recently examined the question, found that even under the most favorable conditions regeneration does not take place if the circumœsophageal nerve-commissure is completely removed with the head, but if a part remains, a new head develops. It has been stated that a new foot regenerates in helicarion, and I have found the foot regenerates also in the fresh-water snails, physa, limnœa and planorbis. If the margin of the shell of a lamellibranch or of a snail is broken off it is renewed by the mantle. The arms of some of the cephalopods are known to regenerate, particularly the hectocotylized arm.

In all the main groups of echinoderms, with one possible exception, regeneration has been found to take place. Probably all starfishes and brittle-stars regenerate their arms, and even if cut in two or more pieces new starfishes develop. The crinoids regenerate lost arms, and even parts of the disc; also the visceral mass. The holothurians have very remarkable powers of regeneration. In some forms regeneration takes place if the animals are cut in two, or even in more than two pieces. The remarkable phenomena of evisceration that take place in certain holothurians, if they are roughly handled, or kept under unfavorable conditions, are well known, and have been described by a number of writers. It has even been suggested that the holothurian may save itself by offering up its viscera to its assailant! Unfortunately for this view, it has been found that the viscera are unpalatable, at least to sea-anemones and to fishes. Ludwig and Minchin suggest that the throwing off of the cuvierian organs, that are attached to the cloaca, is a defensive act, and if carried too far, according to the latter writer, the viscera may also be lost. The holothurians have remarkable recuperative powers and may regenerate new viscera in a very short time. The sea urchins, form, perhaps, an exception in this group since there are no records of their regenerative power, but no doubt this is because they have not been as fully investigated as have other forms.

In the vertebrates we find that the lower forms, amphioxus, petromyzon and sharks, have not been studied in regard to their regenerative power. In the teleostean fishes, the fins of a number of forms have been found to regenerate. It is probable that this takes place in most members of the group.

In the amphibia we find a large number of forms that regenerate their limbs and tail, and other parts of the body, but limitations appear in certain forms. The rapid regeneration of the legs in the smaller urodeles has been often described. In larger

forms it takes place more slowly, at least in large forms having large legs. In proteus the regeneration may extend over a year and a half, and in necturus it takes more than a year to make a new limb, at least in animals in confinement. In the large form, amphiuma, that has extremely small legs regeneration takes place much more rapidly than in a form like necturus having much larger legs.

In amphiuma the feet are not used by the animal as organs of locomotion, since they are too small and weak to support the heavy body. They can be moved by the animal in the same way that the feet are moved in other forms, and yet are useless for progression. It is said by Schreiber that the regeneration of the legs of *Triton marmoratus* is relatively very slight as compared with that of other forms. Fraisse also found in this form that an amputated leg did not grow again, only a deformed stump being produced. The tail, also, is said to regenerate to only a slight extent, but, so far as I know, there is nothing peculiar in the life of this form that makes it less liable to injury than other large urodeles.* Weismann cites the case of proteus that is said also to regenerate less well than do other forms. It lives in the caves of Carniola, where there are few other animals that could attack or injure it, and to this immunity is ascribed its lack of power of regeneration, yet Goette states that he observed a regenerating leg in this form, but that the process was not complete after a year and a half. In necturus also, which is not protected in any way, regeneration is equally slow. Frogs are unable to regenerate their limbs, although they are sometimes lost, but the larval tadpole can regenerate at least its hind legs. In the reptiles the tail regenerates, though this is accomplished more readily in some groups than in others, but at present we do not know of any connection between this condition and the liability of certain forms to injury. Turtles and snakes do not regenerate their tails. I do not know of any observations on crocodiles.

In birds, the legs and wings are not supposed to have the power to regenerate,* but in two forms † at least the beak has been found to possess remarkable powers of regeneration. There are a few very dubious observations in regard to the regeneration in man of superfluous digits that had been cut off.‡

These examples might be added to by others in the groups cited, and also by examples taken from the smaller groups of the animal kingdom, but those given will suffice, I think, to show that the power to regenerate is characteristic of entire groups rather than individual species. When exceptions occur, we do not find them to be forms that are obviously protected, but the lack of regeneration can rather be accounted for by some peculiarity in the structure of the animal. If this is borne in mind as well as the fact that protected and unprotected parts of the same animal regenerate equally well, there is established, I think, a strong case in favor of the view that there is no necessary connection between regeneration and liability to injury. We may, therefore, leave this side of the question and turn our attention to another consideration.

It will be granted without argument that the power of replacement of lost parts is of use to the animal that possesses it, especially if the animal is liable to injury. Cases of usefulness of this sort are generally

*I do not know whether this animal was kept long enough to make it certain that the legs do not regenerate.

* A statement to the contrary quoted in Darwin's 'Animals and Plants under Domestication,' is doubted by Darwin himself.

† The stork and the fighting cocks.

‡ See Darwin, *loc cit.*

spoken of as adaptations. The most remarkable fact in connection with these adaptive responses is that they take place, in some cases at least, in parts of the body where they can never, or at most very rarely, have taken place before, and the regeneration is as perfect as when parts liable to injury regenerate. Another important fact is that in some forms the regeneration is so slow that if the competition amongst the animals was very keen, those with missing legs, or eyes, or tails, would certainly succumb; yet if protected they do not fail to regenerate. If, therefore, the animal can exist through the long interval that must elapse before the lost part regenerates, we can not assume that the presence of the part is of vital importance to the animal and hence its power to regenerate could scarcely be described as the result of a 'battle for existence,' and without this principle 'natural selection' is powerless to bring about its supposed result.

It is extremely important to observe that some cases, at least, of regeneration are not adaptive. This is shown in the case where a new head regenerates at the posterior end of the old one in *Planaria lugubris*, or where a tail develops at the anterior end of a posterior piece of an earthworm, or when an antenna develops in place of an eye in several crustacea. If we admit that these results are due to some inner laws of the organisms, and have nothing to do with the relation of these organisms to the surroundings, may we not apply the same principle to other cases of regeneration in which the result is useful?

So firm a hold has the Darwinian idea of utilitarianism over the thoughts of those who have been trained in this school, that whenever it can be shown that a structure or a function is useful to an animal it is without further question set down as the result of the death struggle for existence. A number of writers, being satisfied that the process of regeneration is useful to the animal, have forthwith supposed that, *therefore*, it must have been acquired by natural selection. Weismann has been cited as an example, but he is by no means alone in maintaining this attitude. It would be entirely out of place to enter here into a discussion of the Darwinian theory, but it may be well worth while to consider it in connection with the problem of regeneration.

We might consider the problem in each species that we find capable of regenerating; or if we find this too narrow a field for our imagination we might consider the process of regeneration to have been 'acquired by selection in the lower and simpler forms' and trace its subsequent progress as it decreased in the course of phylogeny 'in correspondence with the increase in complexity of organization' or with the decrease of exposure to injury. At the risk of following the narrower point of view I shall confine the discussion to the possibility of regeneration being acquired, or even augmented, through a process of natural selection in any particular species.

The opportunity to regenerate can only occur if a part is removed by accident or otherwise. On the Darwinian theory we must suppose that of all the individuals of each generation that are injured *in exactly the same part of the body*, only those have survived or have left more offspring that have regenerated. In order for selection to take place it must be supposed that amongst these individuals injured *in exactly the same region* regeneration has been better in some forms than in others, and that this difference is, or may be, decisive in the competition of the forms with each other. The theory does not inquire into the origin of this difference between individuals, but rests on the assumption of individual differences in the power to regenerate, and assumes that

these differences can be heaped up by the survival and inbreeding of the successful individuals, *i. e.*, it is assumed that, by this picking out or selection through competition in each generation of the individuals that regenerate best, the process will become more and more perfectly carried out in the descendants until at last each part has '*acquired*' the power of complete regeneration.

There are so many assumptions in this argument, and so many possibilities that must be realized in order that the result shall follow, that, even if the assumptions were correct, one might still remain skeptical in regard to the possibilities ever becoming realized. If we examine somewhat more in detail the conditions necessary to bring about this supposed process, we shall find ample grounds for doubt, and even, I think, for denial, that the results could ever have been brought about in this way.

In the first place the assumption that the regeneration of an organ can be accounted for as a result of the selection of those individual variations that are somewhat more perfect, rests on the grounds that such variations occur, for the injury itself that acts as a stimulus is not supposed to have any direct influence on the result, *i. e.*, for better or worse. All that natural selection pretends to do is to build up the complete power of regeneration by selecting the most successful results in the right direction. In the end this really goes back to the assumption that the tissue in itself has a fuller power to regenerate completely in some individuals than in others. It is just this difference, if it could be shown to exist, that is the scientific problem. But, even leaving this criticism to one side, since it is very generally admitted, it will be clear that in many cases most of the less complete stages of regeneration that are assumed to occur in the phyletic series could be, in each case, of very little use to the individual. It is only the completed organ that can be used; hence the very basis of the argument falls to the ground. The building up of the complete regeneration by slowly acquired steps, that can not be decisive in the battle for existence is not a process that can be explained by the theory.

There is another consideration that is equally important. It is assumed that those individuals, that regenerate better than those that do not, survive, or at least have more descendants; but it should not be overlooked that the individuals that are not injured (and they will belong to both of the above classes) are in even a better position than are those that have been injured and have only incompletely regenerated. The uninjured forms, even if they did not crowd out the regenerating ones, which they should do on the hypothesis, would still intercross with them, and in so doing bring back to the average the ability of the organism to regenerate. Here we touch upon a fatal objection to the theory of natural selection that Darwin himself came to recognize in the later editions of the 'Origin of Species,' viz., that unless a considerable number of individuals in each generation show the same variation the result will be lost by the swamping effects of intercrossing. If this be granted, there is left very little for selection to do except to weed out a few unsuccessful competitors, and if the same causes that gave origin to the new variation on a large scale should continue to act, it will by itself bring about the result, and it seems hardly necessary to call in another and questionable hypothesis.

Finally, a further objection may be stated that in itself is fatal to the theory. We find the process of regeneration taking place not only at a few vulnerable points, but in a vast number of regions, and in each case regenerating only the missing part. The leg of a salamander can regenerate from every

level at which it may be cut off. The leg of a crab also regenerates at a large number of different levels, and apparently this holds for all the different appendages. If this result had been acquired through the action of natural selection, what a vast process of selection must have taken place in each species! Moreover, since the regeneration may be complete at each level and in each appendage without regard to whether one region is more liable to injury than is another, we find in the actual facts themselves nothing to suggest or support such a point of view.

If, leaving the adult organism, we examine the facts in regard to regeneration of the embryo, we find again insurmountable objections to the view that the process of regeneration can have been produced by natural selection. The development of whole embryos from each of the first two or first four blastomes can scarcely be accounted for by a process of natural selection, and this is particularly evident in those cases in which the two blastomeres can only be separated by a difficult operation and by quite artificial means. If a whole embryo can develop from an isolated blastomere, or from a part of an embryo without the process having been acquired by natural selection, why apply the latter interpretation to the completing of the adult organism?

Several writers on the subject of regeneration in connection with the process of autotomy (or the reflex throwing off of certain parts of the body) have, it seems to me, needlessly mixed up the question of the origin of this mechanism with the power of regeneration. If it should prove true that in most cases the part is thrown off at the region at which regeneration takes place to best advantage, it does not follow at all that regeneration takes place here better than elsewhere, because in this region a process of selection has most often occurred. The phenomenon of regeneration in the arm of the starfish, that has been described on a previous page shows how futile is an argument of this sort. If, on the other hand, the autotomy is supposed to have been acquired in that part of the body where regeneration takes place to best advantage, then our problem is not concerned with the process of regeneration at all, but with the origin of autotomy. If the attempt is made to explain this result also as the outcome of the process of natural selection acting on individual variations, many of the criticisms advanced in the preceding pages against the supposed action of this theory in the case of regeneration, can also readily be applied to the case of autotomy.

T. H. Morgan.

SOME CONDITIONS INFLUENCING SUCCESS AT SCHOOL.

The law of universal variation as demonstrated by the pupils of our public schools has presented a most difficult problem to the superintendent. He is 'between the devil and the deep sea' in his attempts to give the individual his rights, and at the same time conform to a system which is capable of turning out good material in large quantities. Procrustean beds, with semi-elastic foot-boards are about the best that can be provided for the little folks in the large cities, even under the best conditions. The problem is an important one and far from a satisfactory solution, but we have all confidence in the brains which are brought to bear upon it, and it cannot be very long before some one of the systems which are now in the experimental stage will show itself worthy of more extended adoption. Whatever variety there may be in the attempts to solve this problem of promotion in the schools—for after all, it resolves itself to that—there are certain facts